

Proprioceptive, visual and vestibular thresholds for the perception of sway during standing in humans

Richard Fitzpatrick and D. I. McCloskey

Prince of Wales Medical Research Institute, Randwick, Sydney, NSW 2031 Australia

1. Thresholds for the perception of postural sway induced by gentle perturbations were determined for five normal standing subjects. In this context we understand 'perception' to mean 'able to give a subjective report'. The thresholds for the perception of movements that were equivalent to sway in velocity and amplitude were determined when the available sensory input was limited to only one, or a pair, of the vestibular, visual, and proprioceptive systems. To examine vestibular inputs alone, vision was excluded and the whole body was moved with the ankles in a fixed position. To examine visual inputs alone, the body was kept stationary and a 'room' was moved around the subjects to simulate the relative visual-field movement that occurs during standing. To limit the available sensory input to proprioception from the legs, subjects were held stationary and balanced a load that was equivalent to their own body using their ankles. In this situation, perturbations were applied to the 'equivalent body' and these could only be perceived from the resulting ankle movements. Thresholds for perceiving ankle movements were also determined in the same posture, but with the leg muscles bearing no load.
2. The thresholds for the perception of sway during standing were very small, typically 0.003 rad at a velocity of 0.001 rad s^{-1} , and even smaller movements were perceived as the mean velocity of the sway increased up to 0.003 rad s^{-1} . No difference was found between the thresholds for perceiving forward sway and backward sway. Eye closure during standing did not affect the threshold for perceiving sway.
3. When sensory input was limited to proprioception from the legs, the thresholds for the perception of passive ankle movements were equivalent to the thresholds for the perception of sway during standing with all sensory inputs available. When the leg muscles were relaxed, the thresholds for perceiving ankle movements increased approximately twofold.
4. The visual thresholds for perceiving movement were higher than the proprioceptive thresholds at slower velocities of movement, but there was no difference at higher velocities.
5. Both the proprioceptive and visual thresholds were sufficiently small to allow perception of the sway that was recorded when the subjects stood normally in a relaxed manner. In contrast, the vestibular thresholds were an order of magnitude greater than the visual or proprioceptive thresholds and above the largest sway movements that were recorded during normal standing.
6. When more than one sensory modality was available for perception, subjects performed at a level that was equivalent to the sensory modality that had the greater acuity.
7. These findings indicate that, during normal standing, proprioceptive inputs from the legs provide the most sensitive means of perceiving postural sway. At higher, but not lower, velocities within the range of velocities of normal sway, visual inputs provided similarly sensitive means of perceiving sway. However, large disturbances of posture would be required before vestibular mechanisms could provide perceptual information about body sway, and the present study indicates that the vestibular system plays no part in the perception of sway during normal standing.

Detection of sway during standing is vital to the maintenance of a stable posture, and vestibular, visual or peripheral proprioceptive sensory signals are candidates for providing the nervous system with this information. In an earlier paper we reported reflex responses to small, induced sways that could not be perceived (Fitzpatrick, Taylor & McCloskey, 1992). In the current paper we consider the ability to perceive movement, which requires detection together with sufficient neural processing to be able to report the movement and which provides a measure of sensory acuity. It is known that the vestibular system may contribute to the perception of body orientation and is involved in the control of standing (Guedry, 1974; Bussell, Katz, Pierrot-Deseilligny, Bergego & Hayat, 1980; Young, 1984; Allum & Pfaltz, 1985; Horstmann & Dietz, 1988). Since most postural sway occurs at the ankles (Smith, 1957), signals of ankle rotation from proprioceptive receptors in the legs or feet could provide this information. With sway, there is a relative visual-field rotation about the axis of the ankles in the opposite direction. Information about sway is available from retinal signals and is capable of stabilizing stance (Paulus, Straube & Brandt, 1984).

Movement perception thresholds have been determined for visual, vestibular and proprioceptive systems. The usual test of proprioceptive acuity for joint movements is to displace a limb at a preset velocity and ask subjects to indicate the direction of the movement (Laidlaw & Hamilton, 1937; Hall & McCloskey, 1983; Clark, Burgess, Chapin & Lipscomb, 1985). Subjects can perceive smaller movements as the velocity is increased, and active contraction of the muscles at a joint improves perceptual acuity (Gandevia & McCloskey, 1976; Taylor & McCloskey, 1992). Vestibular thresholds for the perception of body movement have been measured by supporting subjects in different positions while a constant linear or angular acceleration is applied (Walsh, 1960; Clark & Stewart, 1970). Acceleration is the critical variable in these experiments but velocity is also important (Melvill-Jones & Young, 1978). Since it is known that the otoliths respond to static position, vestibular sensibility has also been measured by having subjects reset their position after a small tilt and determining the displacement that produces corrections in the right direction (Mann & Dauterive, 1949). As with joint rotations, subjects can perceive smaller movements as velocity is increased, and this indicates that vestibular inputs provide a movement sense as well as a static position sense. It is known that there are specialized neural mechanisms for detecting movement of visual images (Regan & Beverley, 1978; Nakayama, 1985; Paulus, Straube, Krafczyk & Brandt, 1989), and the ability to perceive movements of a visual target has been investigated extensively. Many factors may affect visual acuity for movement, including eye-target distance, position of the target in the visual field, luminance and contrast. Thresholds for visual perception of displacement, velocity and acceleration have been reported, but these

studies consider movements of a target in the visual field rather than movements of the entire visual field as occurs during standing (Leibowitz, 1955; Gottsdanker, 1956; Regan & Beverley, 1978).

Perception of sway may come from signals related to position, velocity or acceleration, and each sensory system could provide different information about these parameters. Since experimental techniques have differed and because the thresholds may be specific for standing, it is not possible to assess the relative contribution of each to the perception of movements during standing. The present study of normal subjects determined the displacement thresholds for the perception of sway during standing when vestibular, visual and peripheral proprioceptive sensory inputs were all available. In this paper, 'perception' indicates that subjects have detected an event and can reliably report on it. It does not exclude the possibility that 'detection' and processing at a subconscious level can occur with different, lower thresholds – indeed, it is likely that such detection forms the basis of reflex postural control (Fitzpatrick, Taylor & McCloskey, 1992). Thresholds for movement perception were also determined when the available sensory input was limited to only one, or a pair, of the vestibular, visual and proprioceptive mechanisms. It is generally accepted that subjects can report that movement has occurred before they know its direction (Melvill-Jones & Young, 1978; Hall & McCloskey, 1983; Nakayama, 1985), but the direction of a movement must also be perceived if this is to be functionally useful. Subjects in this study were required to identify the direction of imposed movements.

METHODS

Five healthy adults, aged between 24 and 38 years, were subjects in these non-invasive studies of human standing. All had normal visual acuity without correction. The authors were excluded from the study, and the subjects were unaware of any experimental hypotheses. The experiments were designed to determine thresholds for the reliable perception of postural sway when different combinations of vestibular, visual or lower-limb kinaesthetic information were available. The experiments were approved by the institute's human ethics committee.

Set-up

Movements were produced of either (i) the subject's body, (ii) the subject's visual field, or (iii) a load, mechanically equivalent to the body, which subjects used their feet to balance. In each case, the movements were either forward or backward rotations about the axis of the ankles. Subjects were asked to identify the directions of the imposed movements. Below, the experimental preparations are described according to the sources of available sensory input.

Visual, vestibular and proprioceptive signals. Subjects stood on a stable platform with their eyes open. A position-controlled linear servomotor was attached through a weak spring (5 N m^{-1}) to a belt that was fastened around the subject's pelvis (Fig. 1, All). The belt was 75 mm wide and tightened so that the pressure was distributed and relative

pressure changes to the surrounding skin were minimized. The motor, driven by a variable ramp generator, caused the subject to sway either forward or backward. Large disturbances were not necessary to evoke sway: perceptible sway could be evoked by ramps of 100 g over several seconds. It was established by a control experiment that subjects could not perceive the perturbation from the pressure change at the belt. With the belt attached in the same manner to seated subjects, pulls of more than 10 times the rate used in the experiment were required for perception of the pressure change. Body sway was derived by attaching a very weak spring (0.2 N m^{-1}) from the right tibial tuberosity to a force transducer and calibrating the tension to angle. The visual field was a facing wall at 2.5 m and adjacent walls at 0.8 m, both with pictures attached. The 'floor' was a desktop slightly above knee level and the ceiling was approximately 1.5 m above eye level.

Lower-limb proprioceptive. This task simulated standing, but excluded vestibular and visual sensory input as possible contributors to detection of the movement (see Fitzpatrick *et al.* 1992). Subjects were supported upright to prevent body sway and, with their eyes shut, used their feet to balance a near-vertical load that simulated their bodies when standing (Fig. 1, Legs). The load had an axis of rotation co-linear with the axis of the ankles, so that when the servomotor and spring moved the load the ankles rotated and applied the same changing force that would occur during standing. To measure the sway, the strain gauge and spring were attached to the upright load. To examine proprioceptive acuity at the ankle while the leg muscles were relaxed, the weight that simulated the mass of the body was removed and the platform was supported by strong springs. These supported the unloaded frame, requiring no additional support to be applied by the subjects, whose muscles could therefore relax completely. Subjects remained supported with their leg muscles relaxed while the servomotor moved the platform and ankles.

Visual. This set-up simulated the relative movement of the visual field that occurs with body sway about the ankles but in a situation where vestibular and proprioceptive sensory inputs could not contribute to detection of the movement. Subjects stood on a stable platform and were supported to prevent sway. Their visual field was filled entirely by the inside of a large box ($2.6 \times 1.6 \times 1.5 \text{ m}$) which was supported over them (Fig. 1, Eyes). This box was a 'room' with an axis of rotation co-linear with the ankles. The facing and adjacent walls were 1.8 and 0.8 m from the subjects respectively, and had pictures attached. The 'floor' was slightly above knee level and the ceiling approximately 0.4 m above eye level. A light was fixed to the ceiling to maintain brightness. The servomotor moved the room either towards or away from the subjects. The visual-field changes produced when the room moves towards the subject is equivalent to that produced by forward sway of the body when standing. Moving the room away from the subject is equivalent to backward sway. The movement was measured as rotation about the axis of the ankles.

Vestibular. Subjects were blindfolded and supported upright on a rigid, L-shaped platform that prevented ankle movement (Fig. 1, Ears). The servomotor moved the platform and subject together about the axis of the ankles. In this situation, vestibular signals are likely to provide the most significant sensory information about the movement, but it is conceivable that input from mechanoreceptors throughout the body might assist perception.

Paired combinations. Pairs of sensory modalities were also examined. (i) Vestibular plus visual: subjects were supported

on the L-shaped platform but in this series they had their eyes open; this allowed the use of vestibular and visual inputs to perceive the movements but excluded signals related to ankle rotation. (ii) Visual plus proprioceptive: the subject was supported upright to prevent body sway and the movable room was rigidly attached to the equivalent body so that the ankles rotated and the room swayed in unison; visual and lower-limb proprioceptive signals could be used but vestibular cues were excluded. (iii) Vestibular plus proprioceptive: subjects stood on the stable platform with their eyes shut.

Protocol

To test each sensory modality, and each pair of modalities, subjects performed between eighty and one hundred trials. The directions of the pulls were randomized. Frequent rests were allowed to prevent muscle fatigue and to assist with concentration. Each trial began from an identical position by having the subject or the experimenter, aided by a position trace on an oscilloscope, align the position of the body (or equivalent body) to a designated target level. When the subject indicated that he or she was ready, the target display was extinguished and the trial began. Subjects attempted to hold a steady position until the experimenter stopped the trial. Subjects were asked to nominate the direction of any perceived movement (forward or backward) that occurred during the trial, and were not required to distinguish between movements induced by the perturbation and those of normal body sway. They were asked to respond as soon as they were certain they could do so, but were also asked to refrain from guessing: thus, this was not a forced-choice protocol. After a variable delay of between 1 and 5 s from the start of the trial, the servomotor either pulled or released and thereby produced a sway of the body or equivalent movements of the ankles or visual field. The perturbation produced movements with magnitude and velocity that were equivalent to the sway of normal standing. The effects of reaction time at higher velocities were overcome by allowing a 2 s period after the completion of the servomotor displacement during which a response was accepted. The experimenter stopped the trial at this time. Occasionally, subjects readjusted their posture during a trial, and they could cancel such a trial if unsatisfied with their performance in maintaining a steady position.

Failure to respond was recorded as an unperceived movement. Likewise, a response in the direction opposite to the actual direction of sway was recorded as an unperceived movement. If the movement was not perceived, the excursion or velocity of the motor was increased prior to the next trial and, conversely, if the movement was perceived, either the excursion or velocity was reduced. This protocol imposed movements that tended to alternate between perceived and unperceived.

Data collection

Following the start of the perturbation, the movement of the body, or equivalent body, during each trial was recorded at 40 Hz for 5 s and displayed on a computer monitor. Points were chosen at the inflections that corresponded to the beginning and end of a movement and from these the angular displacement and the mean angular velocity of the body, or equivalent body, were calculated (Fig. 2A).

In previous studies that have examined threshold magnitudes for the perception of movement, passive movements with set velocities and displacements were imposed on a limb that was not otherwise free to move

(Laidlaw & Hamilton, 1937; Hall & McCloskey, 1983; Clark *et al.* 1985). A threshold for displacement was calculated for each velocity, sometimes by finding the smallest amplitude that subjects could perceive in 70 % or more movements (Hall & McCloskey, 1983; Clark *et al.* 1985). The present study concerns normal standing, and the movement was imposed with a compliant coupling that permitted normal standing and its accompanying body sway. Since the observed movements were the sum of the perturbation effects and the natural body sway, they were randomly distributed in velocity and displacement. Therefore, a different method was necessary to estimate movement sensibility.

With each imposed movement, displacement was plotted against mean angular velocity (Fig. 2*B*). This created two bivariate populations, one of perceived movements and one of unperceived movements. The points representing perceived

movements tended to have larger displacements and velocities but there was usually an area of overlap with those representing unperceived movements. The 'perceived' points were ordered by polar angle from 0 to 90 deg, and a series of lines was constructed to connect the sequence, thereby forming a discontinuous 'function' (Fig. 2*C*). This was repeated for the 'unperceived' points. A 'threshold curve' that was midway (by polar radius) between the perceived and unperceived functions was calculated with an arbitrarily chosen resolution of 200 points of equal polar angle over the length of the curve. For each experimental trial, this curve separated the perceived and unperceived points and so provided an estimate of the threshold for movement detection (Fig. 2*C*). However, because they provide less information about the threshold, detected points that were 'distant' from the unperceived points (and *vice versa*) were weighted so that they had a lesser influence on

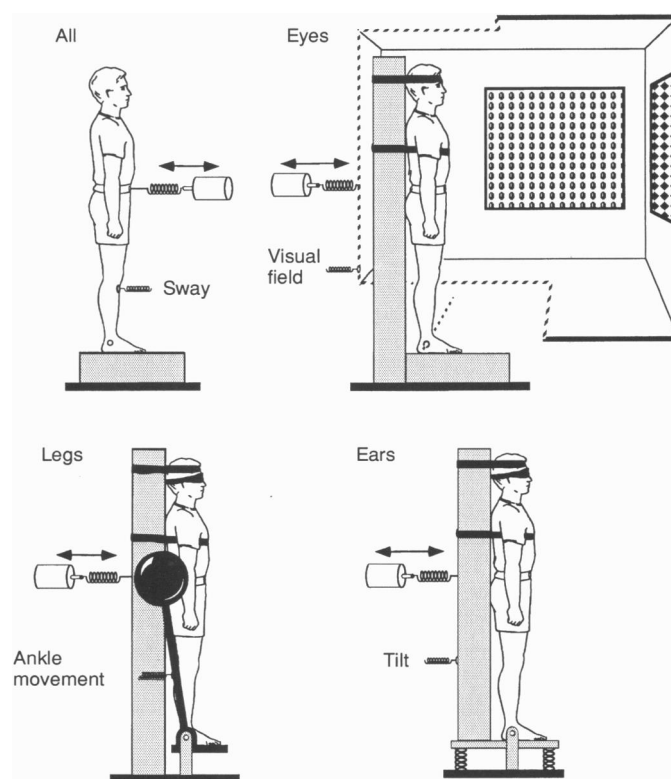


Figure 1. Experimental set-up

All, top left, the subject stood on a stable support with the eyes open. Sway was measured by attaching a very weak spring from the tibial tuberosity to an isometric strain gauge. When the subject was still, and indicated so, a perturbation was applied by a servomotor that was attached through a weak spring to the belt around the pelvis. Eyes, top right, the subject was immobilized to prevent vestibular and proprioceptive inputs and the entire visual field was filled by the inside of a large box ($2.6 \times 1.6 \times 1.5$ m). The servomotor moved the box, either towards or away from the subject, about an axis that was co-linear with the subject's ankles. Legs, bottom left, this set-up excluded relevant vestibular and visual inputs so that the movement could only be perceived with lower-limb proprioceptive inputs. The subject was supported upright, using the feet to balance a weight that was attached to the supporting platform which could rotate about the axis of the ankles. The weight was matched to the subject's weight and its height to the height of the subject's centre of mass. When the servomotor moved the load, the movement was applied to the subject's ankles. Ears, bottom right, the subject was blindfolded and supported upright in the standing position on a rigid L-shaped platform. The servomotor moved the subject about the axis of the ankles but no ankle rotation could occur. With this set-up, vision and lower-limb proprioception were excluded as sources of sensory input.

the threshold line. This was achieved by moving any point that had both adjacent points closer to the origin, and therefore the threshold: its new position arbitrarily chosen as two-thirds of the distance towards the adjacent points, that is, the centroid of a triangle formed by the remote point and its neighbouring closer points (Fig. 2*C*, point X). The assumption was that if both smaller movements were perceived, then the larger movement would almost certainly have been perceived

(*vice versa* for undetected movements). The effects of this procedure were to lessen the displacement of the threshold curve that a sampling bias would introduce, and to smooth the threshold curve. To illustrate typical performances, the threshold curves so constructed for each individual subject were then averaged on a point-by-point basis across all the points in the array to produce a mean threshold curve for the group of subjects. Averaging on a point-by-point basis was

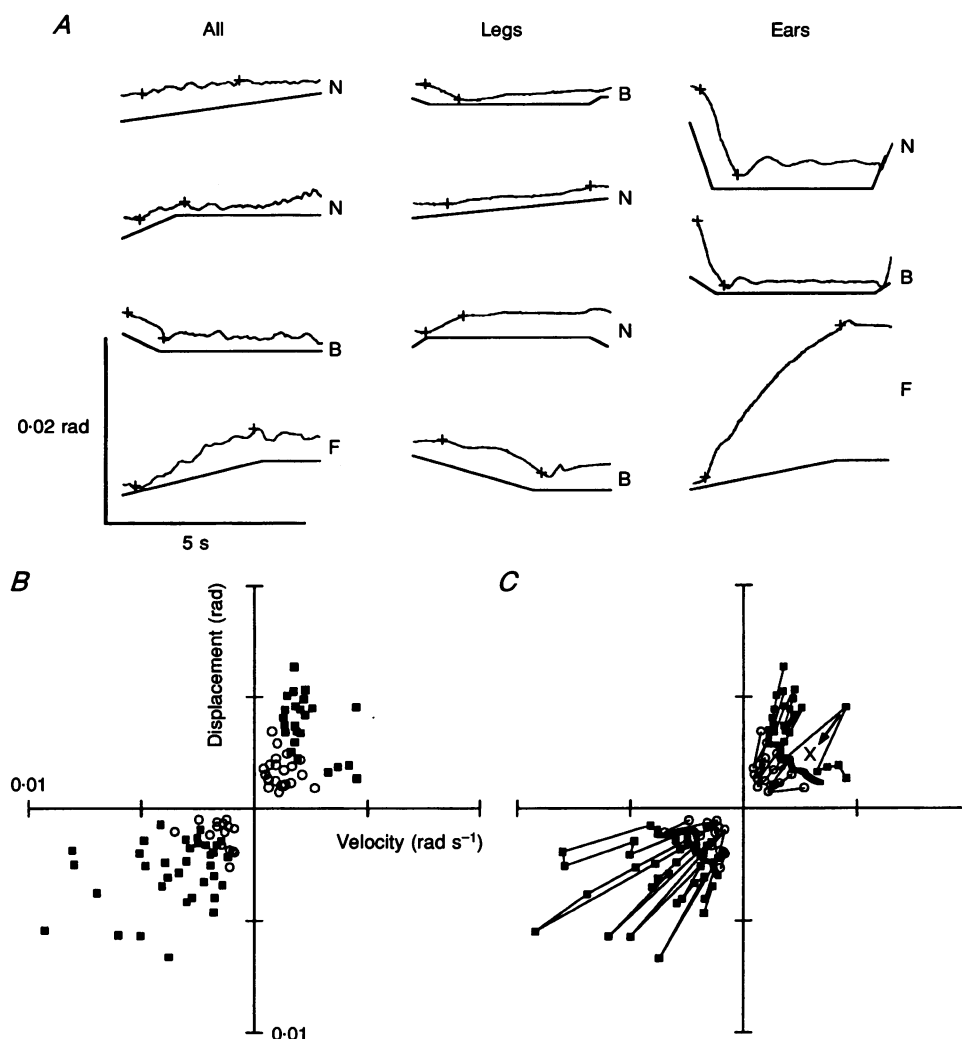


Figure 2. Calculation of threshold curves

A, typical movement records for standing with eyes open (All), lower-limb proprioceptive (Legs), and the vestibular (Ears) protocols. The top tracings show the movement of the subject and, below each, the movement of the motor. Points of inflection were chosen (+) and displacement and mean velocity were calculated. Responses were either forward (F), backward (B) or none (N). *B*, for one subject who was standing with eyes open, the perceived (■) and unperceived (○) movements are plotted as displacement *versus* velocity, with forward movements in the upper quadrant (F) and backward movements in the lower quadrant (B). The perceived points were displaced further from the origin, but there was a region of overlap between the perceived and unperceived points. *C*, for each group, lines have been constructed to join the points, starting at the point with the least polar angle and progressing in order of increasing polar angle. This curve was smoothed without affecting the threshold values by moving points that were 'distant' from the threshold (e.g. the point indicated by the arrow) to a new position that was arbitrarily chosen as two-thirds of the distance towards its neighbouring points. (e.g. the distant point was moved to the position marked X). A threshold curve (thick line) was then calculated as a curve that was midway (by polar length) between the perceived and unperceived curves.

chosen after examining the similarity of results obtained from different subjects.

Having determined individual subjects' threshold curves for the different sensory modalities, it was necessary to decide if these curves were significantly different from each other. An analysis of variance (ANOVA) was applied to selected displacement values from the individual subjects' threshold curves. Sensory modality, subject and direction were chosen as the independent variables, and velocity as a covariate. The displacement values for this analysis were obtained as follows. First, the group, either perceived or unperceived, with the fewest observations was selected. Experimental observations from the selected group that were 'near' the threshold curve were chosen because they provided a more reliable estimate of the true threshold. Observations that were 'distant' from the threshold curve, that is points with both neighbouring points closer to the threshold line, were excluded (see above and Fig. 2). The values selected for the ANOVA were recorded as the displacement values of the threshold curves at the velocities of the chosen 'near' observations from the selected group. This selection procedure meant that at least one 'near' perceived movement and one 'near' unperceived movement were required for each threshold estimate.

In addition, a second technique was used to determine whether differences between the perception thresholds for different experimental tasks were statistically significant. This was to compare the frequency of perceived and unperceived movements within a standard reference region that was defined by limits of velocity and displacement. The reference region, described as the 'threshold domain for standing', was defined for the group of subjects by the area of overlap between perceived and unperceived movements during normal standing (see results below) and is depicted, for forward sway, as the dashed box in Fig. 4. This threshold domain box is bounded by the smallest displacement perceived and the largest displacement unperceived, and the slowest velocity perceived and the fastest velocity unperceived. If performances for a sensory modality were similar to standing then the frequency of perceived movements within this threshold domain would be similar to the frequency of perceived movements during standing and, conversely, a poor performance would produce relatively few perceived movements.

RESULTS

The ability to perceive the direction of antero-posterior sway during standing was determined for five normal subjects. This was compared with their ability to perceive (i) similar body sway without its concurrent visual-field or ankle movement, (ii) visual-field movements alone, and (iii) ankle movements alone.

If they were not fatigued, subjects could maintain stance with imperceptibly small sway for periods of up to 10 s. It was possible to apply small postural perturbations and produce movements that were too small for subjects to perceive (Fitzpatrick *et al.* 1992). On other occasions, subjects were aware that a movement had occurred but were uncertain of its direction and so could not perceive it according to the experimental requirement of specifying direction. If the movement was large enough, subjects

could not distinguish having been pulled forwards from having become aware of naturally occurring sway but, because they could perceive the direction, these were recorded as perceived movements. If still larger perturbations were applied during standing, as well as perceiving the direction, subjects could report that the movement was experimentally induced, presumably because it was beyond the range of expected sway. The perceived (■) and unperceived (○) movements during standing and when only one sensory input was available are plotted for one subject in Fig. 3. Large movements were perceived consistently and small movements were never perceived, but there was a region of overlap where subjects could not reliably perceive the movement and its direction.

Subjects were encouraged to respond only when they were certain of the direction of any movement and, in general, there were few (< 3 % for all subjects, < 4 % for any subject) 'wrong' responses where a movement was perceived but an incorrect direction was specified. This was the case for the standing, visual and proprioceptive protocols, but during the vestibular protocol, large movements frequently caused a wrong response (22 % for all subjects, 29 % for any subject).

To determine if perceptual sensitivity was greater at higher velocities, data were arbitrarily divided into slow (< 0.02 rad s⁻¹) and fast (> 0.02 rad s⁻¹) movements. For all experimental protocols, the proportion of perceived movements was greater at the higher velocities ($P < 0.05$, χ^2 test with Bonferroni's correction for multiple comparisons). Similarly, when the data were divided into small (< 0.02 rad) and large (> 0.02 rad) displacements, the proportion of perceived movements was greater with the larger displacements. For all experimental protocols, there were no significant differences between the ability to perceive forwards or backwards movements (ANOVA and F test or frequency comparison and χ^2 test). The five subjects gave quantitatively similar results for each experimental protocol, and the individual threshold curves and pooled results for forward sway are plotted in Fig. 4.

When standing with the eyes open, subjects could perceive the direction of very small movements (Fig. 4, All). At slow velocities of approximately 0.001 rad s⁻¹, subjects reliably perceived all forward and backward movements greater than 0.003 rad. At higher velocities of approximately 0.002 rad s⁻¹, all subjects reliably perceived movements of 0.002 rad. Occasionally, movements as small as 0.001 rad were perceived. A 'threshold domain for standing' was defined for the group of subjects in which perceived and unperceived movements overlapped and is depicted, for forward movements, by the dashed outlines in Fig. 4. This domain consisted of two rectangular areas (forward and backward movements) that were bounded by (i) the smallest displacement perceived by any subject, (ii) the largest displacement not perceived by any subject, (iii) the lowest velocity perceived, and (iv) the highest velocity not perceived. Movements within this domain were equally

perceived and unperceived (51 % and 49 % respectively, $n = 220$) for standing with the eyes open. This threshold domain for standing was used as a reference for frequency comparisons of responses when only single sensory modalities were available.

When subjects used their feet to balance an equivalent mechanical body, only receptors in the legs could provide sensory information about the movement. In this situation, the displacement and velocity of the ankle movements were similar to standing (Fig. 4, Legs). There was no significant difference between the frequency of perceived movements when standing (51 %, $n = 220$) and perceived ankle movements during this equivalent task (50 %, $n = 161$) for the ankle movements that fell within

the threshold domain for standing. One subject performed slightly better during the 'legs only' task than with standing – another did not perform as well. When the leg muscles were relaxed and not actively balancing the body or the load, subjects were less likely to perceive movements of the same size. Within the threshold domain, only 34 % ($n = 188$) of movements were correctly perceived with the leg muscles relaxed compared with 50 % ($n = 161$) when they were contracted ($P < 0.001$, χ^2 test).

The ability to perceive the direction of movements of the entire visual field appeared to be more dependent on the velocity of the movement (Fig. 4, Eyes). At velocities of 0.003 rad s^{-1} subjects reliably perceived a visual-field movement of 0.001 rad – similar in size to the smallest

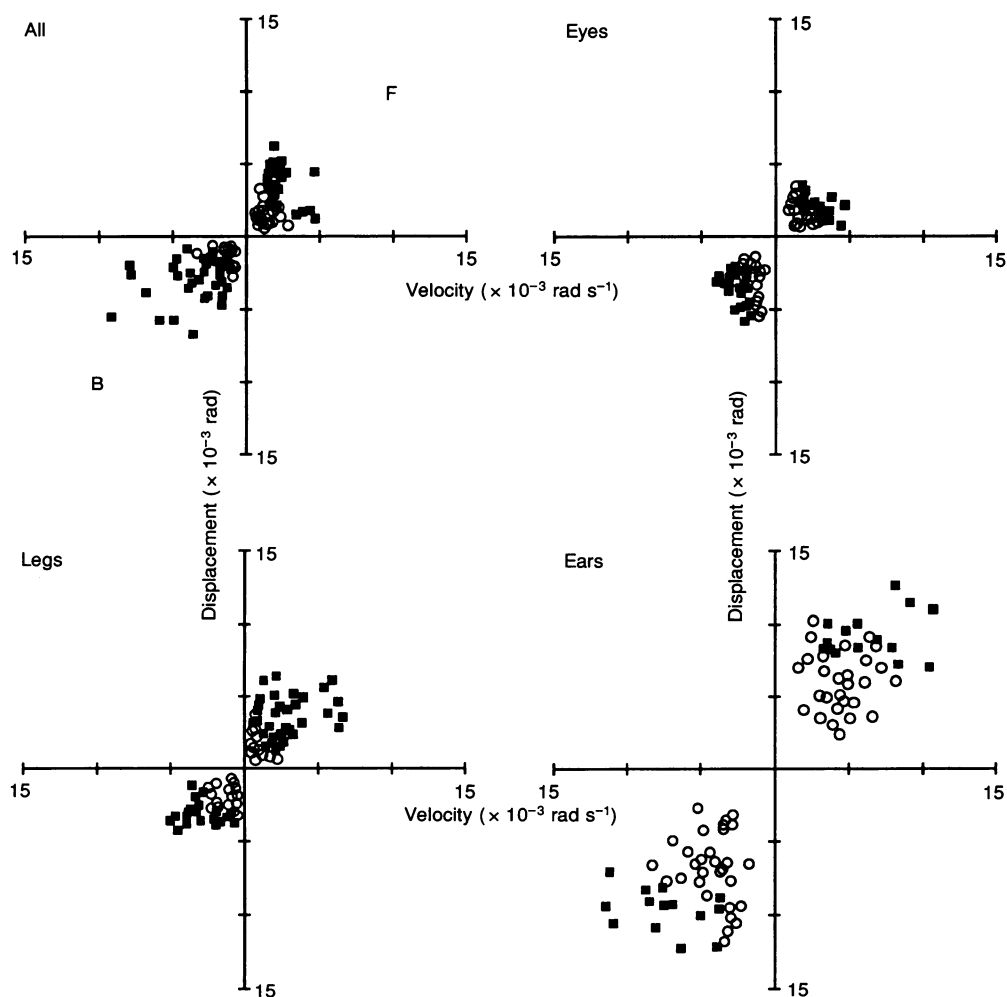


Figure 3. Results from one subject for the four experimental protocols where only one, or every, sensory modality was available

Displacement is plotted against velocity for forward (F) and backward (B) movements, and for perceived (■) and unperceived (○) movements. When only visual input was available (Eyes) or only lower-limb proprioceptive information was available (Legs) the subject perceived movements of similar size to those that were perceived when visual, vestibular and proprioceptive inputs were all available during normal standing (All). In contrast, when only vestibular inputs were available (Ears), the velocity and the displacement of a movement had to be much larger for the movement to be perceived.

perceived body sway or ankle movement. However, the visual performance deteriorated at slower velocities so that no subject perceived visual-field movements smaller than 0.001 rad. Every subject perceived ankle movements at velocities below their limit for perceiving equivalent visual-field movements. Within the threshold domain for standing, only 29 % ($n = 156$) of visual-field movements were correctly identified compared with 51 % ($n = 220$) during standing ($P < 0.001$, χ^2 test).

If ankle movement is prevented and the body is rotated about the axis of the ankles, the vestibular system is likely to be the main, and perhaps only, source of sensory information about body movement. However, it is conceivable that exteroceptors throughout the body may contribute. Another potential bias in the vestibular-only result may arise from the larger (22 %) incidence of wrong responses. Although guessing was discouraged, a similar number of correctly guessed responses would cause the

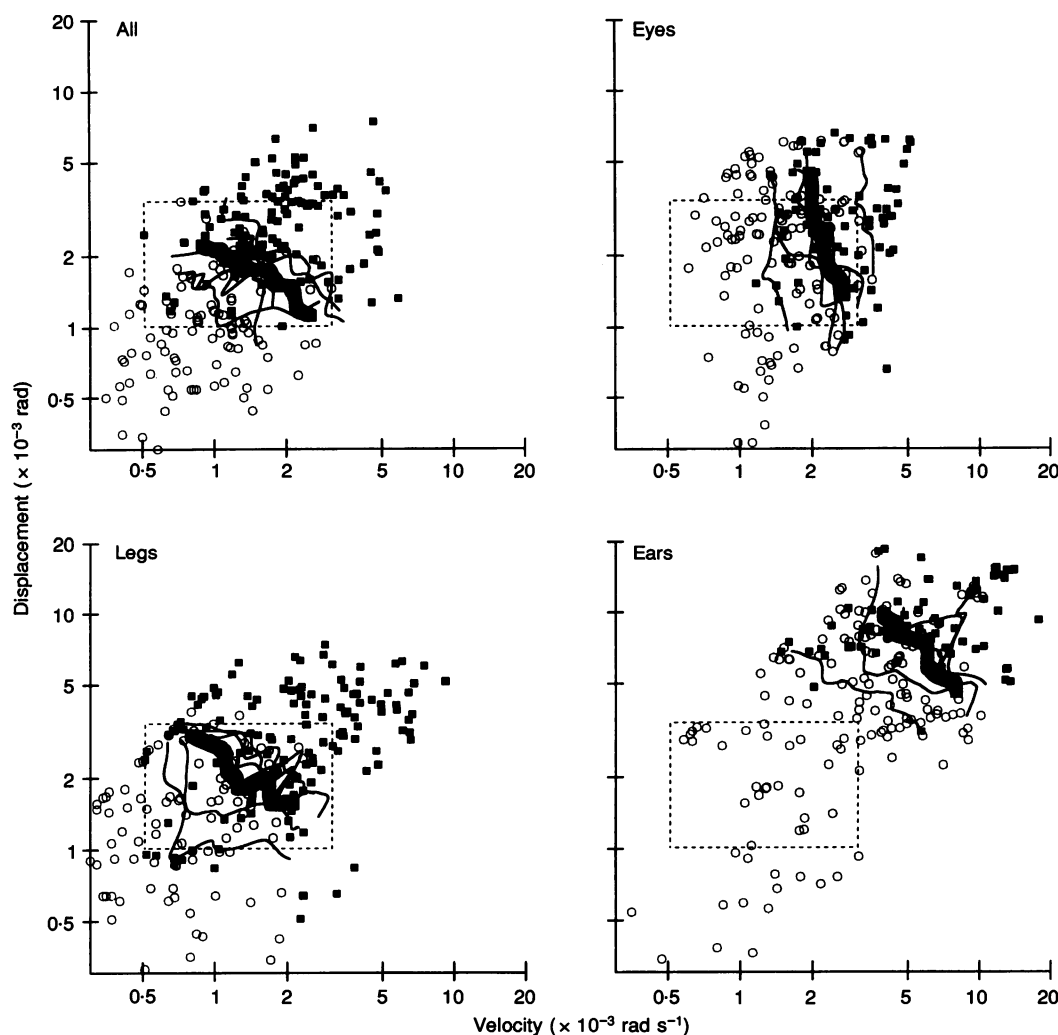


Figure 4. Plots on log scales of pooled results for all five subjects

Only forward movements are shown. In each situation, the group-average threshold curves (thick lines) pass through the region of overlap of perceived (■) and unperceived (○) movements. The group-average thresholds are the average of the five threshold curves for individual subjects (thinner lines). When standing with the eyes open (All), the dashed box is bounded by (i) the smallest displacement, (ii) the slowest velocity that was perceived, (iii) the largest displacement, and (iv) the fastest velocity that was not perceived. The region bounded by this box, termed the threshold domain for standing, had equal frequencies of perceived (51 %) and unperceived (49 %) movements during standing. To compare performance when only one sensory modality was available, the same box is superimposed on the other graphs. When only lower-limb proprioceptive inputs were available (Legs), there were also equal frequencies of perceived (50 %) and unperceived (50 %) movements. With only visual inputs available (Eyes), a smaller proportion (34 %) of movements that fell within the box were perceived, and the slope of the visual threshold curve shows that this was due to a poorer visual performance at slower velocities. When only vestibular inputs were available (Ears) none of the movements within the box was perceived.

estimate of the threshold to be lower than the actual threshold. Therefore this experimental set-up determines the *best* performance of the vestibular system although actual performance may be below this. For the perception of sway, the vestibular system was significantly inferior to either lower-limb kinaesthesia or vision. The experimental equipment and the 5 s duration of the movement limited large movements and it was not possible to reach perceptible levels for velocities below 0.002 rad s^{-1} . When tested on this apparatus, subjects and visitors to the laboratory were surprised, on opening their eyes, at how far they could be moved slowly without being aware of it. For the movements seen in the study, the average velocity required for vestibular perception was approximately 5 times that necessary for kinaesthetic perception. Without accounting for this greater velocity, the displacement necessary for perception was 4 times that for

perception by kinaesthetic mechanisms. Of the forty-nine movements (27 forward, 22 backward) that fell within the threshold domain for standing (Fig. 4, Ears), none were correctly identified when only vestibular inputs were available compared with 51 % during standing ($P < 0.001$, χ^2 test).

Threshold curves were calculated for individual subjects to separate the perceived from the unperceived movements (see Methods). An analysis of variance of data from these curves, and the frequency comparisons described above, both revealed differences between sensory modalities at similar significance levels. The average of the threshold curves for the five subjects coincides with the region of overlap between perceived and unperceived movements for the group (Fig. 4). These curves provide a population estimate of the limit of movement sensibility for each sensory modality. When plotted together (Fig. 5), they

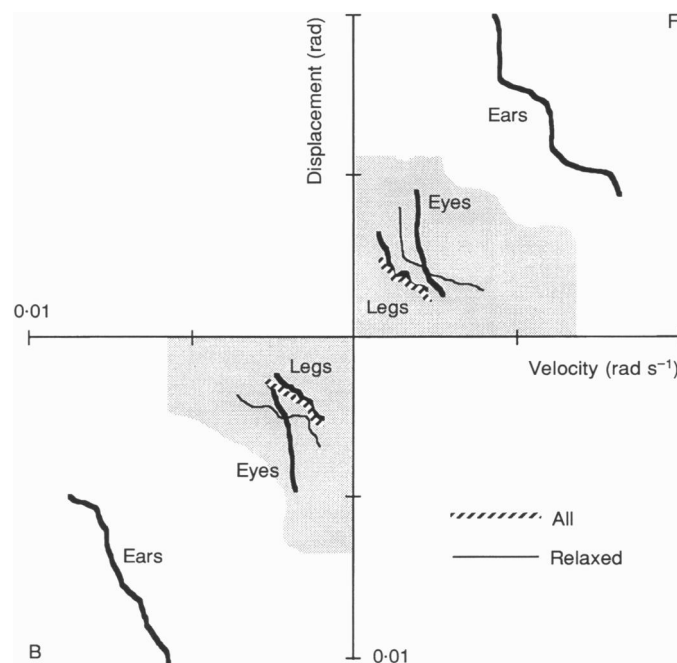


Figure 5. Comparison of the thresholds for different sensory modalities and with the size of the sway that normally occurs during standing

Group-average results are shown for forward (F) and backward (B) sway. During normal standing when vestibular, visual and proprioceptive information were all available (interrupted line), the threshold for perception of sway when vestibular, visual and proprioceptive information was available (interrupted line) coincided with the threshold for perceiving ankle movements when only lower-limb proprioceptive inputs were available (Legs, thick line). When the leg muscles were relaxed (thin line), the threshold for perceiving ankle movements was higher than when the leg muscles were actively contracted and subjects balanced their equivalent mechanical bodies. The visual threshold (Eyes, thick line) was higher than the threshold for perceiving sway during standing, and there was a marked increase in the threshold as the velocity of the movements became slower. The shaded areas indicate the limits of the velocities and displacements of sway that were recorded when each subject stood relaxed for periods of 80 s. The proprioceptive and visual thresholds were within this region, which indicates that these inputs could provide what normal subjects perceive of the sway that occurs during standing. However, if only vestibular inputs were available, the threshold for perceiving movement (Ears, thick line) fell well beyond the region of naturally occurring sway. For each sensory modality and for standing, there was no difference between the thresholds for perceiving forward and backward movements.

illustrate that: (i) the vestibular system has relatively poor acuity for the perception of sway, (ii) proprioceptive information from the legs alone can account for the ability to perceive sway during standing, (iii) contraction of the calf muscles during standing enhances the acuity of proprioceptive mechanisms, and (iv) vision can provide sensory information about movements of equivalent magnitude, but is limited at velocities below 0.002 rad s^{-1} .

The largest antero-posterior movements during 80 s of normal standing were determined for each subject, and these were bounded by the shaded region in Fig. 5. All sway movements that had a duration between 250 ms and 5 s are included in this region. This corresponds to sway frequencies between 0.01 and 2 Hz and, therefore, it accounts for the sway that occurs during normal standing (Aggashyan, 1972). These movements were all below the threshold curve for the vestibular system but much of the normal sway was above the perception curves for the proprioception and vision. The conclusion from this must be that normal subjects cannot perceive normal body sway with their vestibular systems, and so must rely on lower-limb proprioception or vision to perceive sway.

Subjects' ability to perceive sway when standing with their eyes open was equivalent to their ability to perceive movements of the ankles using lower-limb proprioceptive sensory inputs alone. Shutting the eyes while standing did not produce a significant change in subjects ability to perceive sway (Fig. 6, left). For each protocol, acuity for movement perception was equivalent to the acuity of the

better sensory modality available. Likewise, when the moving room was attached to the mechanical body so that visual and lower-limb proprioceptive input was available, subjects' ability to perceive movements was not significantly different from the situation where proprioceptive mechanisms alone were available (Fig. 6, middle). An apparent slight departure from this pattern for combined modalities was for the combination of vestibular and visual inputs compared with visual inputs alone. Subjects were able to perceive slightly smaller movements of the visual field alone than movements of the body when the eyes were open and the ankle movement was prevented ($P < 0.05$ by ANOVA, Fig. 6, right).

DISCUSSION

When vestibular, visual and peripheral proprioceptive sensory inputs were available during standing, subjects could perceive very small antero-posterior sway movements, typically 0.001 – 0.002 rad (0.06 – 0.12 deg) of rotation at the ankles. This displacement threshold for perception of sway during standing was equivalent to the threshold for perception of passive movements of the loaded ankle joints: this was obtained when subjects were supported upright and used the calf muscles to balance a mechanical load that was equivalent to the body, a situation in which only lower-limb proprioceptive sensory input was available. Thus, the availability of vestibular and visual input when the body sways about the ankles,

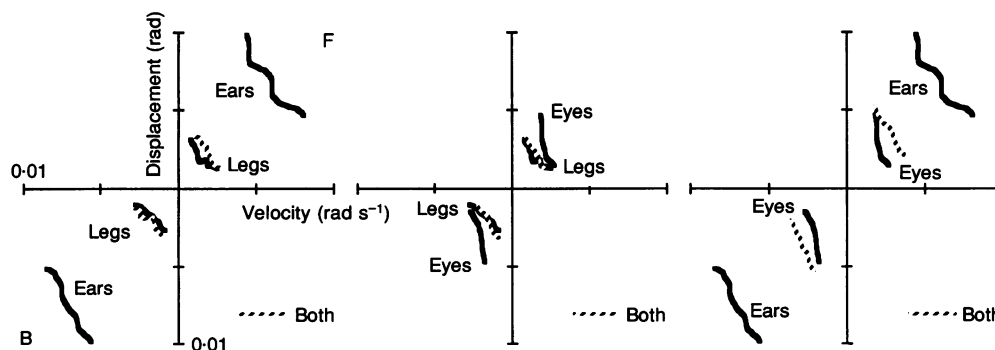


Figure 6. Comparison of the thresholds when only one or a pair of sensory modalities were available

Group-average results are shown for forward (F) and backward (B) sway. Left, the thresholds for perception of movement are shown when only lower-limb proprioceptive input (Legs), and when only vestibular input (Ears), was available. When subjects stood with their eyes shut, sensory input was available from both of these sources, and the threshold coincided with the proprioceptive threshold (Both, interrupted line). Similarly, in the middle graph, the lower-limb proprioceptive threshold is compared with the visual-only threshold (Eyes). When subjects were balanced their equivalent mechanical bodies and the visual field rotated with the ankles, both visual and proprioceptive information were available and, in this situation, the threshold (Both) coincided with the threshold for perceiving movement when only proprioceptive information was available. Right, when vestibular and visual inputs were available (Both) the threshold, although closer to the visual threshold than the vestibular threshold, was significantly different from the visual threshold ($P < 0.05$ by ANOVA). It is possible that this was caused by differences in the visual target distances in the two situations.

and the absence of these inputs when vision is excluded and the body remains stationary and an equivalent load sways about the ankles, made no difference to subjects' ability to perceive the sway. The displacement threshold for perception of the relative visual-field movements that accompany the faster sway movements that occur during standing ($> 0.002 \text{ rad s}^{-1}$) was equivalent to the threshold for perception of the sway during standing or the threshold for perception of passive ankle movements. However, at lower velocities ($< 0.002 \text{ rad s}^{-1}$), subjects were less able to perceive the visual-field movements than equivalent movements of the ankles. The displacements and velocities of sway that occurred during relaxed standing were frequently above the proprioceptive and visual thresholds so that either input would be sufficient for the perception of sway during standing, although visual inputs would be less effective at lower velocities. Notably, this was not the case for vestibular inputs, where the displacement threshold for the perception of movements about the axis of the ankles was many times greater than the visual or proprioceptive thresholds, and greater than the largest displacements that occurred during standing. It must be concluded, therefore, that vestibular mechanisms play no part in the perception of normal body sway during standing.

Kinaesthetic signals about ankle movements could provide information about body sway. Cutaneous receptors adjacent to the ankle, joint receptors in the capsule of the ankle and receptors in the leg muscles could potentially contribute to sensations of ankle movement. However, smaller ankle movements were perceived when the calf muscles were actively contracted rather than relaxed, and this improved kinaesthetic acuity cannot be attributed to cutaneous receptors around the ankle joint because they would not be affected by soleus contraction. Although most joint receptor firing occurs at the extremes of the range of movement, some receptors in human subjects have their firing rates modulated by movements in the mid-range (Burke, Gandevia & Macefield, 1988) and can evoke perceptions of joint movement (Macefield, Gandevia & Burke, 1991). However, in the normal situation where muscle, joint and cutaneous receptors are all available, joint receptors probably play no more than a supportive or, at best, duplicative role to that of muscle receptors in kinaesthesia (Ferrell, Gandevia & McCloskey, 1987; Clark, Grigg & Chapin, 1989). In the present study, the thresholds for perception of ankle rotation were very small and sufficient to account for the perception of sway when standing. However, even when the leg muscles were relaxed the thresholds were less than one-fifth of those reported by Clark *et al.* (1985) for the relaxed human ankle joint. Apart from the contraction of the ankle plantar flexors during standing, several other differences may contribute to the better performance in the present study: (i) the movement was imposed on both ankles simultaneously, (ii) a threshold rather than a 70 % perception level is reported, and (iii) subjects in this study

were upright so that the ankles supported the weight of the body and a resulting rise in intra-articular pressure may have made joint receptors more sensitive to movement (Ferrell *et al.* 1987).

It is likely that subjects use signals from muscle spindles to perceive the movements (Goodwin, McCloskey & Matthews, 1972; Hall & McCloskey, 1983). In the cat soleus, muscle spindles respond to a stretch of $10 \mu\text{m}$ or 0.002% of muscle length (Matthews & Stein, 1969) and there is evidence that human spindles are similarly sensitive (Newsom Davis, 1975). Human soleus fascicles have an average length of 31 mm and the insertion of the Achilles tendon is approximately 43 mm from the axis of the ankles (Yamaguchi, Sawa, Moran, Fessler & Winters, 1990) so that theoretically some spindles in the soleus could respond to movements of less than 0.0002 rad . This spindle sensitivity would be more than sufficient to account for the proprioceptive threshold seen during standing. However, firing of a single muscle spindle does not cause a perception of movement (Macefield *et al.* 1991), and it is likely that the population response of spindles from the leg muscles is the effective sensory input. Human soleus contains a high density of muscle spindles (Levy, 1963), and during standing the soleus is continuously active while other leg muscles remain silent or only intermittently active (Joseph & Nightingale, 1952). Muscle contraction recruits spindle afferents that were not previously firing and increases the resting firing rate of afferents that were previously firing (Burke & Eklund, 1977; Burke, Hagbath & Skuse, 1978; Vallbo, Hullinger & Nordh, 1981), presumably by co-activation of α - and γ -motoneurons. The total signal that arises from the muscle spindles will be increased during muscle contraction because more spindles will respond to the stretch, and this is probably the cause of the lower perception thresholds. The angular displacement thresholds found here for active contraction of the leg muscles are similar to those reported for the elbow when the arm muscles are contracted (Taylor & McCloskey, 1992), and about one-tenth of those when the arm muscles are relaxed (Hall & McCloskey, 1983).

During standing, the force of the leg muscles and distribution of pressure under the feet will vary with the sway of the body, and both of these need to be considered as sources of sensory input. Golgi tendon organs that are associated with the leg muscles will have an increased dynamic sensitivity because of the muscle contraction (Appenteng & Prochazka, 1984), but are still relatively insensitive to external stretch when compared with their high sensitivity to contraction of associated motor units. In a related study (Fitzpatrick *et al.* 1992), reflex electromyographic responses in the soleus were evoked by imposed movements that were below the threshold levels for perception reported here. The effect of this reflex muscle contraction on tendon organ firing may provide an indirect sensory input related to sway. Both fast- and slow-adapting mechanoreceptors in the feet are likely to change

their firing during small postural movements. For a typical subject, a sway of 0.002 rad can be calculated to produce a differential force between the heel and sole of approximately 300 g. At first sight this appears to be a large value but, because of the large weight of the body, it represents less than a 1 % change in the background forces at the receptor sites and this is less than the Weber fraction of 0.05 for weight discrimination (Ross & Brodie, 1987). Another possible sensory input when balancing the equivalent mechanical body could come from pressure changes on the back from the supports of the body. However, subjects were strapped firmly to the support, and the large surface area of the back and the long lever arm of the support compared with the size and length of the feet would cause minimal pressure changes on the back for these small disturbances. Greater pressure changes on the back would have occurred during the larger movements of the vestibular-only protocol and, because these movements were unperceived, we are persuaded that remote receptors did not contribute to perception during the proprioceptive-only protocol.

As with the proprioceptive and visual thresholds, the vestibular thresholds depended on the velocity of the imposed movement. The displacement required for perception decreased as the mean velocity increased. This suggests that subjects perceived movement rather than a changed position. It is known that the otoliths are sensitive to the static orientation relative to the gravitational field and to the inertial reaction forces that are generated by the acceleration component of movement. Differentiation of the static position signal within the central nervous system could allow the position signal to be perceived as movement. Signals related to acceleration and deceleration, which would be approximately proportional to the mean velocity of a movement, will also contribute to the perception of sway. These acceleration-related signals may explain the higher incidence of 'wrong' responses during the vestibular-only protocol, because deceleration at the end of a forward sway and acceleration at the start of a backward sway would be expected to produce identical phasic responses from the otoliths. Normal subjects have a similar difficulty in the subjective perception of the direction of vertical movements of the body (Melvill-Jones & Young, 1978), as most people will have experienced when a lift commences to move. Phasic signals of acceleration may originate from the semicircular canals but it is thought that they have little responsiveness at the low frequencies of body sway (Nashner, Shupert, Horak & Black, 1989) and are involved more with the high-frequency task of eye-head co-ordination. In the controlled conditions of these experiments the head was stationary relative to the body and this is likely to be the optimal arrangement for vestibular perception of sway.

For visual targets on a stationary background, perception of movement over a long duration (> 1 s) is inferred from relative position changes but, over a shorter

duration (< 1 s), specific movement-responsive mechanisms are used (Cohen & Bonnet, 1972; Scobey & Johnson, 1981). It is likely that both mechanisms are used for perception because sway movements that lasted more than 1 s and less than 1 s were perceived. Displacement thresholds for perceiving target movements are approximately 2 min of arc for foveal vision and up to 10 times this for peripheral vision (Regan & Beverley, 1983). However, these thresholds are for simple, single-point movements that are perpendicular to the optic axis. The shift of the retinal image of a target point that is moving parallel to the optic axis will only reflect the perpendicular component of the movement vector. Movement of the entire visual field, as occurs during standing, will cause an array of such images that either converge or diverge. Thus, images of target objects will change in size, and there will be a changing disparity between the left and right retinal images. Either of these stimuli – optic flow or stereopsis – are perceived as a movement in depth (Beverley & Regan, 1975; Regan & Beverley, 1978). The changing disparity might also be detected by efference-copy mechanisms as the eyes track a moving target. To perceive sway movements of 0.002 rad (equivalent to 3 mm of eye movement), theoretical calculations based on visual thresholds (Paulus *et al.* 1989) suggest that to perceive a changing target size, a stationary visual target would need to be 20–30 cm from the subject. This was not the case for the moving room or the normal standing situations where visual targets were 1–2 m from the subjects. Similar theoretical calculations show that for changing-disparity mechanisms, subjects should not perceive movements of 0.002 rad until the target distance was less than approximately 50 cm. Therefore, the results of this study show that perception of antero-posterior sway is about 3 times better than is predicted by thresholds for perceiving movement of a point target, and support the finding by Paulus *et al.* (1989) that postural sway is attenuated by visual targets that are further displaced than the theoretically predicted limit for visual stabilization. It appears that visual thresholds derived from point-target experiments do not provide reliable estimates of thresholds for perceiving movement in depth of the entire visual field, which is the visual stimulus that occurs during standing.

The visual thresholds described here are specific for the conditions of the experiment. Since visual thresholds vary with target distance, lower thresholds could be expected for targets that are closer than those used here. Indeed, a lower threshold was seen when the room moved and the subject was stationary (Fig. 6, Eyes only) than when the subject was moved and the room was stationary (Fig. 6, Ears and Eyes). This may result from the target distance being closer in the former situation (approximately 1.8 m compared with 2.5 m to the facing walls). Visual movement thresholds should be higher in a situation where there were distant visual targets and lower for close-up targets, but both the distances used in this study are common in many

everyday situations. Also, for faster movements than seen here, such as those which may result from rapid perturbations to posture, the visual thresholds may be lower than described here. The range of velocities used in these experiments are representative of the movements that occur during normal standing (Fig. 5). In the present study, subjects could fix on a visual target and thereby maximize their ability to perceive movements but, in the everyday situation where gaze moves about the visual field, a greater amount of neural processing would be required to extract the sway-related signal. Consequently, it is possible that visual thresholds may be higher than is indicated by these results.

It might be expected that if additional sensory inputs were available (say, visual plus proprioceptive instead of proprioceptive alone), the threshold for movement perception could be lowered. Our results do not support this proposal. When more than one sensory modality was available, subjects performed no better than they would have if only the modality with the greater sensitivity were available. This suggests that subliminal inputs from two sensory sources are not mutually facilitatory in a way that can augment perceptual experience and that subjects use the most sensitive input available. When multiple sensory inputs are available, all but the most sensitive input are redundant. As the threshold for perceiving sway during standing is not altered by eye closure it is likely that visual information is redundant as a source of information for perceiving sway during normal standing. However, visual and vestibular inputs are likely to be more significant sources of information about sway when proprioceptive information is unreliable as it is when standing on an unstable support or when visual information is enhanced as occurs with very close visual targets.

REFERENCES

- AGGASHYAN, R. V. (1972). On spectral and correlation characteristics of human stabilograms. *Agressologie* **13**, 63–69.
- ALLUM, J. H. J. & PFALTZ, C. R. (1985). Visual and vestibular contributions to pitch sway stabilization in the ankle muscles of normals and patients with bilateral vestibular deficits. *Experimental Brain Research* **58**, 82–94.
- APPENTENG, K. & PROCHAZKA, A. (1984). Tendon organ firing during active muscle lengthening in awake, normally behaving cats. *Journal of Physiology* **353**, 81–92.
- BEVERLEY, K. I. & REGAN, D. (1975). The relation between sensitivity and discrimination in the perception of motion-in-depth. *Journal of Physiology* **249**, 387–398.
- BURKE, D. & EKLUND, G. (1977). Muscle spindle activity in man during standing. *Acta Physiologica Scandinavica* **100**, 187–199.
- BURKE, D., GANDEVIA, S. C. & MACEFIELD, G. (1988). Responses to passive movement of receptors in joint, skin and muscle of the human hand. *Journal of Physiology* **402**, 347–361.
- BURKE, D., HAGBATH, K.-E. & SKUSE, N. (1978). Recruitment order of human spindle endings in isometric voluntary contractions. *Journal of Physiology* **285**, 101–112.
- BUSSEL, B., KATZ, R., PIERROT-DESEILLIGNY, E., BERGEGO, C. & HAYAT, A. (1980). Vestibular and proprioceptive influences on the postural reactions to a sudden body displacement in man. *Progress in Clinical Neurophysiology*, vol. 8, *Spinal and Supraspinal Mechanisms of Voluntary Motor Control and Locomotion*, ed. DESMEDT, J. E., pp. 310–322. Karger, Basel, Switzerland.
- CLARK, B. & STEWART, J. D. (1970). Thresholds for the perception of angular acceleration about the three major body axes. *Acta Otolaryngologica* **69**, 231–238.
- CLARK, F. J., BURGESS, R. C., CHAPIN, J. W. & LIPSCOMB, W. T. (1985). Role of intramuscular receptors in the awareness of limb position. *Journal of Neurophysiology* **54**, 1529–1540.
- CLARK, F. J., GRIGG, P. & CHAPIN, J. W. (1989). The contribution of articular receptors to proprioception with the fingers in humans. *Journal of Neurophysiology* **61**, 186–193.
- COHEN, R. L. & BONNET, C. (1972). Movement detection thresholds and stimulus duration. *Perceptual Psychophysics* **12**, 269–272.
- FERRELL, W. R., GANDEVIA, S. C. & MCCLOSKEY, D. I. (1987). The role of joint receptors in human kinaesthesia when intramuscular receptors cannot contribute. *Journal of Physiology* **386**, 63–71.
- FITZPATRICK, R. C., TAYLOR, J. L. & MCCLOSKEY, D. I. (1992). Ankle stiffness of standing humans in response to imperceptible perturbations: reflex and task-dependent components. *Journal of Physiology* **454**, 533–547.
- GANDEVIA, S. C. & MCCLOSKEY, D. I. (1976). Joint sense, muscle sense and their combination as position sense, measured at the distal phalangeal joint of the middle finger. *Journal of Physiology* **283**, 493–499.
- GOODWIN, G. M., MCCLOSKEY, D. I. & MATTHEWS, P. B. C. (1972). The contribution of muscle afferents to kinaesthesia shown by vibration-induced illusions of movement and by the effects of paralysing joint afferents. *Brain* **95**, 705–748.
- GOTTSCHALKER, R. M. (1956). Detection of acceleration of target motion. *Psychology Bulletin* **53**, 477–487.
- GUEDRY, F. E. (1974). Psychophysics of vestibular sensation. In *Handbook of Sensory Physiology*, vol. VI, 2, ed. KORNHUBER, H. H., pp. 1–154. Springer, Berlin, Heidelberg, New York.
- HALL, L. A. & MCCLOSKEY, D. I. (1983). Detections of movements imposed on finger, elbow and shoulder joints. *Journal of Physiology* **335**, 519–533.
- HORSTMANN, G. A. & DIETZ, V. (1988). The contribution of vestibular input to the stabilization of human posture: a new experimental approach. *Neuroscience Letters* **95**, 179–184.
- JOSEPH, J. & NIGHTINGALE, A. (1952). Electromyography of muscles of posture: leg muscles of males. *Journal of Physiology* **117**, 484–491.
- LAIDLAW, R. W. & HAMILTON, M. A. (1937). A study in thresholds of apperception of passive movement among normal control subjects. *Bulletin of the Neurological Institute of New York* **6**, 268–273.
- LEIBOWITZ, H. W. (1955). The relation between the rate threshold for the perception of movement and luminance of various durations of exposure. *Journal of Experimental Psychology* **49**, 209–214.
- LEVY, R. (1963). The relative importance of the gastrocnemius and soleus muscles in the ankle jerk of man. *Journal of Neurology, Neurosurgery and Psychiatry* **26**, 148–150.
- MACEFIELD, G., GANDEVIA, S. C. & BURKE, D. (1991). Perceptual responses to microstimulation of single afferents innervating joints, muscles and skin of the human hand. *Journal of Physiology* **429**, 113–129.
- MANN, C. W. & DAUTERIVE, H. J. (1949). The perception of the vertical. I. The modification of non-labyrinthine cues. *Journal of Experimental Psychology* **39**, 700–707.

- MATTHEWS, P. B. C. & STEIN, R. B. (1969). The sensitivity of muscle spindle afferents to small sinusoidal changes in length. *Journal of Physiology* **200**, 723–743.
- MELVILL-JONES, G. & YOUNG, L. R. (1978). Subjective detection of vertical acceleration: a velocity dependent response? *Acta Otolaryngologica* **85**, 45–53.
- NAKAYAMA, K. (1985). Biological image motion processing: a review. *Vision Research* **25**, 625–660.
- NASHNER, L. M., SHUPERT, C. L., HORAK, F. B. & BLACK, F. O. (1991). Organization of posture controls: an analysis of sensory and mechanical constraints. *Progress in Brain Research* **80**, 411–418.
- NEWSOM DAVIS, J. (1975). The response to stretch of human intercostal muscle spindles studied *in vitro*. *Journal of Physiology* **249**, 561–579.
- PAULUS, W. M., STRAUBE, A. & BRANDT, T. (1984). Visual stabilization of posture: physiological stimulus characteristics and clinical aspects. *Brain* **107**, 1143–1163.
- PAULUS, W., STRAUBE, A., KRAFCZYK, S. & BRANDT, T. (1989). Differential effects of retinal target displacement, changing size and changing disparity in the control of anterior/posterior and lateral body sway. *Experimental Brain Research* **78**, 243–252.
- REGAN, D. & BEVERLEY, K. I. (1978). Looming detectors in the human visual pathway. *Vision Research* **18**, 415–421.
- REGAN, D. & BEVERLEY, K. I. (1983). Visual fields for frontal plane motion and for changing size. *Vision Research* **23**, 673–676.
- ROSS, H. E. & BRODIE, E. E. (1987). Weber fractions for weight and mass as a function of stimulus intensity. *Quarterly Journal of Experimental Psychology* **39A**, 77–88.
- SCOBEY, R. P. & JOHNSON, C. A. (1981). Displacement thresholds for unidirectional and oscillatory movement. *Vision Research* **21**, 1297–1302.
- SMITH, J. W. (1957). The forces operating at the human ankle joint during standing. *Journal of Anatomy* **91**, 545–564.
- TAYLOR, J. L. & MCCLOSKEY, D. I. (1992). Detections of slow movements imposed at the elbow during active flexion in man. *Journal of Physiology* **457**, 503–513.
- VALLBO, A. B., HULLINGER, M. & NORDH, E. (1981). Do spindle afferents monitor joint position in man? A study with active position holding. *Brain Research* **204**, 209–213.
- WALSH, E. G. (1960). Perception of linear motion following unilateral labyrinthectomy: variation of threshold according to the orientation of the head. *Journal of Physiology* **153**, 350–357.
- YAMAGUCHI, G. T., SAWA, A. G. U., MORAN, D. W., FESSLER, M. J. & WINTERS, J. M. (1990). A survey of human musculotendon actuator parameters. In *Multiple Muscle Systems*, ed. WINTERS, J. M. & WOO, L.-Y., pp. 717–773. Springer-Verlag, New York.
- YOUNG, L. R. (1984). Perception of the body in space: mechanisms. In *Handbook of Physiology*, section I, vol. III, ed. BROOKHART J. M., MOUNTCASTLE, V. B., DARIAN-SMITH, I. & GEIGER, S. R., pp. 229–256. American Physiological Society, Bethesda, MD, USA.

Acknowledgements

This work was supported by the National Health and Medical Research Council of Australia.

Received 24 May 1993; accepted 23 November 1993.